

MAXIMUM DIVING DEPTH IN FLEDGLING BLUE-FOOTED BOOBIES: SKILL DEVELOPMENT AND TRANSITION TO INDEPENDENCE

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ABSTRACT.—We evaluated maximum diving depth and time spent at the nest of fledgling Blue-footed Boobies (*Sula nebouxii*) at Isla El Rancho, Sinaloa, in the Gulf of California, Mexico. Within three consecutive 10-day post-fledgling intervals, maximum diving depth was highly variable, but was not affected by sex, weight, or body condition. During the first days of post-fledgling flight, maximum diving depth increased rapidly. By the second week after first flight, the plunge-dives of juveniles were almost as deep as those of adults. Parental care and attachment to the nest lasted several additional weeks (up to 40 days after first flight). Although their diving capacity rapidly reached a level similar to that of the adults, it appeared that juvenile boobies took much longer in acquiring other foraging skills. Received 1 August 2005, accepted 5 July 2006.

The speed with which juvenile birds acquire foraging abilities has important implications for the evolution of life histories (Wheelwright and Templeton 2003). It has been hypothesized that parental care continues until young birds acquire mobility and foraging skills adequate for survival. Additional parental care improves the survival of the offspring, but decreases long-term survival of the parents (Burger 1980).

Juvenile birds face major challenges in learning how to identify foraging areas and developing foraging techniques as the period of parental care ends (Burger 1980, Wheelwright and Templeton 2003). The study of newly volant birds can help elucidate the process of such learning. However, this is complicated in the wild, as fledglings can move freely through the colony site. Most of the few studies on the subject have focused on passerines, which have a rather short transition to independence (Moreno 1984, Wheelwright and Templeton 2003). In seabirds, the development of foraging skills and its relationship to parental care are not well known (Yoda et al. 2004). We are aware of only one such seabird study (Brown Booby, *Sula leucogaster*), although the birds were raised by humans (Yoda et al. 2004), which could have interfered with social learning processes. Even less is known about possible intersexual differences

in the acquisition of foraging skills (Wheelwright et al. 2003).

The Blue-footed Booby (*S. nebouxii*) is a sexually dimorphic seabird: females are larger than males at fledging (Drummond et al. 1991). Parental care continues for a 6-week, post-fledgling period (Nelson 1978). During this period, young birds fly out to sea but return to their nests, where they continue receiving food from the parents. In this study, we determined the maximum diving depths (MDD) of wild fledgling Blue-footed Boobies to (1) examine the ontogeny of MDD and compare it with the diving depths achieved by adults, and (2) examine the relationship between the development of diving skills and sexually related size dimorphism.

METHODS

Field work was conducted at Isla El Rancho (25° 10' N, 108° 23' W), a sandy, 120-ha island in the south-central Gulf of California, Mexico, at the mouth of Bahía de Santa María–La Reforma—a large coastal lagoon. The colony studied was located on the northeastern part of the island among 4-m-high sand dunes. About 500 pairs of Blue-footed Boobies nested in an area of <1 ha, with a maximum density of 0.6 nests/m².

Between January and May 2004, we visited the island 12 times for periods of 5 days and monitored 100 nests and 108 chicks that we had marked with unique combinations of color bands. During each visit, we checked the nests daily, and weighed and measured (culmen, ulna, and tarsus) all banded chicks every other day. Sex was determined from the length

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of ulna at fledging (males = 191–207 mm; females = 213–233 mm; Drummond et al. 1991). Fledging (age at first flight) was inferred when a bird with complete juvenile plumage left its nest site and returned with clean feet (feet were covered with excrement before the first trip to sea). For most birds, we could estimate the exact age at fledging (estimates were ± 2 days in some cases).

From 20 April to 26 May, we estimated MDD by attaching a capillary tube (Tygon, 8 mm internal diameter; Burger and Wilson 1988) to the lower side of a booby's central rectrix. Tubes were recovered one day after application. A total of 99 capillary tubes produced usable data: 67 from fledglings (48 individuals, 15 of which provided data for more than one date), 17 from adult males, and 15 from adult females. In addition, we estimated the amount of time that young spent at their nests by monitoring 38 nests hourly during 14-hr diurnal periods.

We tested the data for normality and homocedasticity with Kolmogorov-Smirnov and Levene's tests, respectively, for every group to be compared. We used parametric procedures when both requirements were met. We grouped the MDD data for post-fledging juveniles into 5-day age intervals. We then conducted a Mann-Whitney *U*-test to compare the MDD attained by male and female fledglings for each 5-day period.

We used a mixed-model ANOVA-ANCOVA for comparing 5-day periods (normality: $D = 0.17$ – 0.39 ; homocedasticity: $F_{4,39} = 0.98$, $P = 0.42$) to evaluate the possible effects of ontogeny on MDD. The number of days since first fledging was included as a covariate, with the 5-day periods as the fixed factor. Multiple flights of the same bird in 10-day intervals (1–10, 11–20, and ≥ 21 days after fledging) were compared with *t*-tests for dependent samples.

We found no significant differences between adult male and female MDD (3.4 ± 2.1 m and 3.6 ± 1.6 m, $n_1 = 15$ and $n_2 = 17$, respectively; $t = 0.33$, $P = 0.73$; normality: $D = 0.22$ and 0.23 , respectively; homocedasticity: $F_{1,31} = 1.7$, $P = 0.26$). Therefore, we pooled the MDD of both sexes to compare adult MDD with that of juveniles that had fledged at least 15 days previously. We tested for age-related differences in MDD using a *t*-test (normality: $D = 0.19$ and 0.13 , respec-

tively; homocedasticity: $F_{1,49} = 3.96$, $P = 0.55$).

We used linear regressions to assess whether MDD might be a function of weight or body condition. Residuals from the regression of weight on culmen length were used as a body condition index. Using residuals of a regression between weight and body measurements as an index of condition is adequate when measurement errors and variations in body size are low (Schulte-Hostedde et al. 2005); the major assumption to be met is that the relationship between variables is linear, which was the case in our study ($r^2 = 0.73$, $P < 0.001$). To explore the relationship between days since first flight and time spent at the nest, we used a mixed ANOVA-ANCOVA model, with gender serving as the fixed factor and days since fledging included as a covariate. All statistical tests were considered significant at $\alpha = 0.05$, and reported values are means $\pm$ SD.

RESULTS

Female Blue-footed Booby chicks reached their maximum pre-fledging weight ($2,071 \pm 125.2$ g) between 60 and 75 days of age, while males reached it ($1,628 \pm 117.5$ g) between 60 and 70 days of age. Females were significantly heavier than males ($t_{49,54} = 18.43$, $P < 0.001$). After reaching their maximum weight, female chicks lost 8.5% of their weight and weighed $1,830$ g $\pm$ 72.2 at first flight, whereas males lost 7% and weighed $1,470$ g $\pm$ 63.5 . Males began to fly earlier than females (83.4 ± 2.64 and 87.9 ± 3.8 days of age, $n_1 = 23$, $n_2 = 19$, respectively; $U = 67$, $P < 0.001$). MDD within any given period was highly variable (Fig. 1), and there were no statistical differences between male and female fledglings (1–5 days after first flight: $n_1 = 9$, $n_2 = 6$, $U = 19$, $P = 0.34$; 6–10 days: $n_1 = 6$, $n_2 = 9$, $U = 16$, $P = 0.38$; 11–15 days: $n_1 = 7$, $n_2 = 9$, $U = 25.5$, $P = 0.52$; 16–20 days: $n_1 = 4$, $n_2 = 6$, $U = 11$, $P = 0.83$).

We did not detect an effect of date on MDD, per se ($F_{1,38} = 3.31$, $P = 0.10$), but despite great within-interval variability, MDD increased with time since first flight throughout the first 15 days of flight (0–5 days = 1.68 ± 0.66 m, 6–10 days = 2.69 ± 0.81 m, 11–15 days = 3.02 ± 0.53 m; $F_{4,39} = 3.64$, $P = 0.012$; Fig. 1). By 16–20 days (3.11 ± 0.76

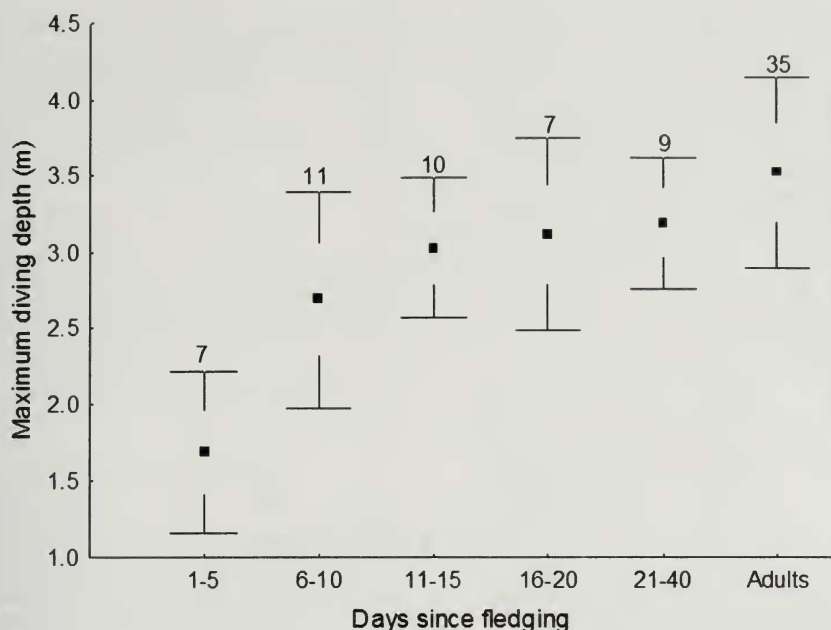


FIG. 1. Maximum diving depth of Blue-footed Boobies increased rapidly during the first 15 days after their first flight at Isla El Rancho, Sinaloa, Mexico, 2004. Fledglings then dived almost as deep as adults. Means $\pm$ SE (white zone) and 95% confidence intervals (whiskers) are shown. Sample size is indicated above whiskers.

m) and 21–40 days (3.18 ± 0.55 m; Fig. 1) since flight, MDD stabilized. The 15 juveniles for which we had >1 MDD value (there were 2 values for 9 birds and >2 for 6 birds) exhibited a similar tendency: during the first 10 days after fledging, dives were shallower than they were during the 11–20 day interval (1–10 days = 2.12 ± 0.70 m and 11–20 days = 3.03 ± 0.90 m, $t_{12} = -2.44$, $P = 0.032$). Birds for which we had >2 records made shallower dives during the first 10 days after fledging than they did ≥ 21 days post-fledging (1–10 days = 1.94 ± 0.35 m and ≥ 21 days = 3.42 ± 0.69 m, $t_4 = -5.05$, $P = 0.007$); there were no significant differences between the two later periods (11–20 days = 2.64 ± 0.71 m and ≥ 21 days = 2.90 ± 0.96 m, $t_7 = -0.51$, $P = 0.62$).

MDD of juveniles that had flown for at least 15 days did not differ from that of adult birds (2.99 ± 0.75 m and 3.51 ± 1.88 m, respectively, $t_{54} = -1.27$, $P = 0.26$). Weight was not correlated with diving depth within sex (males: $P = 0.71$; females: $P = 0.90$). The regression between MDD and body condition also was not significant ($P = 0.23$).

Juvenile birds progressively reduced their

time at the nest after their first flight ($r^2 = 0.33$, $P < 0.001$), with no differences between males and females ($F_{1,29} = 0.11$, $P = 0.73$). After 25 days of flight, some individuals left the nest for at least the entire daylight period. Other young birds remained at their nests for >40 days (Fig. 2).

DISCUSSION

Blue-footed Booby parents reduce their provisioning to offspring just before the nestlings take their first flights (*sensu* Nelson 1978; JAC-G unpubl. data). This reduction may stimulate fledging and encourage the fledglings to develop foraging skills away from their nest. Juveniles make their first plunge dives on their first day of flight (every recovered capillary tube showed evidence of immersion, including four that were attached to birds just prior to their first flight).

Clearly, 15 days of learning were enough for juveniles to dive almost as deep as adults. Based on our observations, the fledglings made their first plunges at low angles and from low heights. As the days passed, the birds increased the plunge height and dives became more vertical. During the first days

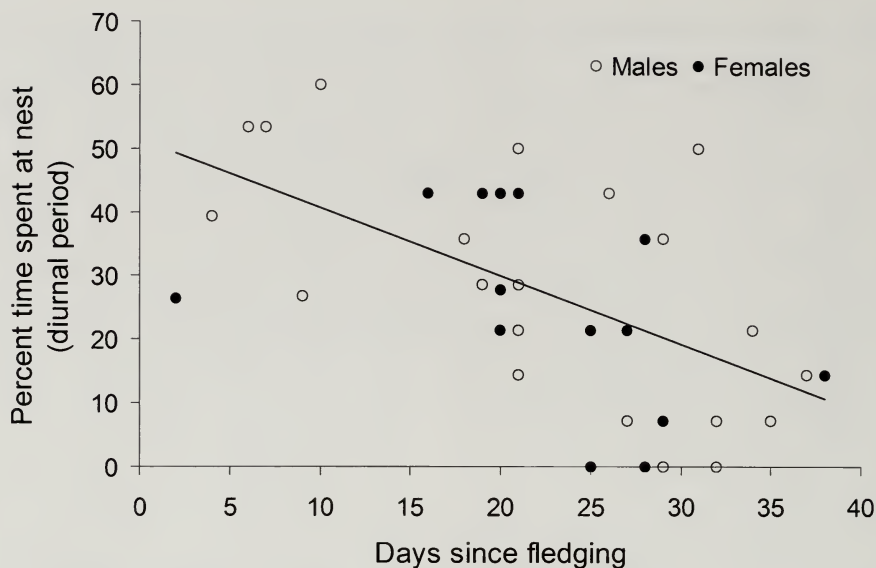


FIG. 2. The percent of diurnal time fledgling Blue-footed Boobies spent at the nest decreased with time since their first flight ($r^2 = 0.33$, $P < 0.001$) at Isla El Rancho, Sinaloa, México, 2004. This relationship is described by the equation $t_n = 0.5147 - 0.107 \times \text{days since fledging}$, where t_n = percentage of diurnal time at nest.

after initiation of flight, fledglings also tended to fly in groups around the island, suggesting that social interactions might facilitate their development of diving and, perhaps, foraging skills.

For several weeks after their first flight, fledglings continued begging for food from their parents. Juveniles of other species usually cease begging when foraging for themselves becomes more profitable (Moreno 1984, Heinsohn 1991, Wheelwright and Templeton 2003); thus, the young birds in our study apparently required several additional weeks to become adequate foragers. Similar to other sulids (Burger 1980, Yoda et al. 2004), the Blue-footed Boobies at El Rancho exhibited gradual separation from their parents. Based on our observations, we hypothesize that there are two periods in the development of foraging skills: (1) an initial rapid improvement in the depth attained during plunge-dives, followed by (2) improvement in other behaviors, such as locating and capturing prey. Presumably, once birds begin catching fish, begging frequency and presence at the nest decrease. Some juveniles apparently achieved this level of independence at 25 days

after fledging, while others required >40 days to do so.

It is unlikely that temporal changes in the depth at which prey were found affected our recorded MDD in fledglings. Our data did not exhibit any effects of date, and fledglings did not exhibit much synchrony in dates of first flight that could confound our data. Some fledglings were already independent by the time others began to fly and, in some cases, >2 months had passed between early- and late-fledging birds. We did not find evidence of temporal patterns in adult MDDs.

Despite the Blue-footed Booby's distinct sexual dimorphism in size and gender-influenced differences in growth and date of first flight (Torres and Drummond 1999; this study), we found no gender differences in MDD. Given the limitations of capillary tubes, however, further study of the relationship between sexual dimorphism in size and booby diving performance is warranted. It seems that fledgling Blue-footed Boobies develop plunge-diving skills and attain MDDs similar to those of adults relatively quickly. However, this does not imply that juvenile feeding success and/or foraging performance

is equivalent to that of adults. Their nest attendance and insistent begging for long periods indicate that foraging for themselves, along with developing prey-finding and prey-capturing skills, delays the full independence of young Blue-footed Boobies.

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